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PARASITES OF NATIVE AND NONNATIVE FISHES OF THE LITTLE COLORADO RIVER, GRAND CANYON, ARIZONA

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ABSTRACT: A 2-yr, seasonal, parasitological study of 1,435 fish, belonging to 4 species of native fishes and 7 species of nonnative fishes from the lower Little Colorado River (LCR) and tributary creeks, Grand Canyon, Arizona, yielded 17 species of parasites. These comprised 1 myxozoan (*Henneguya exilis*), 2 copepods (*Ergasilus arthrosis* and *Lernaea cyprinacea*), 1 acarine (Oribatida gen. sp.), 1 piscicolid leech (*Myzobdella lugubris*), 4 monogeneans (*Gyrodactylus hoffmani*, *Gyrodactylus* sp., *Dactylogyrus extensus*, and *Ligictaluridus floridanus*), 4 nematodes (*Contracaecum* sp., *Eustrongylides* sp., *Rhabdochona* sp., and *Truttaedacnitis truttae*), 3 cestodes (*Bothriocephalus acheilognathi*, *Corallobothrium fimbriatum*, and *Megathylacoides giganteum*), and 2 trematodes (*Ornithodiplostomum* sp. and *Posthodiplostomum* sp.). *Rhabdochona* sp. was the only adult parasite native to the LCR. Infection intensities of *Ornithodiplostomum* sp. and *B. acheilognathi* were positively correlated with length of the humpback chub *Gila cypha*. Adult helminths showed a high degree of host specificity, except *B. acheilognathi*, which was recovered from all fish species examined but was most abundant in cyprinids. Abundance of *B. acheilognathi* in the humpback chub was highest in the fall and lowest in the summer in both reaches of the LCR. There was no major taxonomic difference in parasite assemblages between the 2 different reaches of the river (LC1 and LC2). Parasite community diversity was very similar in humpback chub, regardless of sampling site or time. The parasite fauna of the LCR is numerically dominated by *B. acheilognathi* and metacercariae of *Ornithodiplostomum* sp. The richest and most diverse component community occurred in a nonnative species, the channel catfish *Ictalurus punctatus*, but infracommunity species richness was highest in a native host, humpback chub.

The closure of Glen Canyon Dam (Fig. 1) in 1963 had a profound effect on the physical nature and ecology of the Colorado River in Grand Canyon, transforming a once seasonally warm, turbulent, muddy river into one that is perennially cold and relatively clear (National Academy of Sciences, 1991). The system has been further altered by the introduction of at least 24 species of nonnative fishes (Valdez et al., 2004), some of which may be affecting native fish populations (Minckley, 1991; Marsh and Douglas, 1997; Fuller et al., 1999). The native fish fauna in Grand Canyon today comprises only 4 species, i.e., 2 catostomids (bluehead sucker *Catostomus discobolus* Cope and flannelmouth sucker *C. latipinnis* Baird and Girard) and 2 cyprinids (speckled dace *Rhinichthys osculus* Girard and endangered humpback chub *Gila cypha* Miller).

Nonnative fishes have also introduced potentially pathogenic fish parasites into the system. Two such parasites, the Asian fish tapeworm *Bothriocephalus acheilognathi* Yamaguti, 1934 and the anchor worm *Lernaea cyprinacea* Linnaeus 1761, have been found in native and nonnative fishes of the Colorado River and its tributaries in this region (Carothers et al., 1981; Brouder and Hoffnagle, 1997; Clarkson et al., 1997; Hoffnagle and Cole, 1999). These studies also indicated that the 2 parasites were more abundant in the Little Colorado River (LCR), the major, relatively unaltered tributary of the Colorado River in Grand Canyon. The LCR has become increasingly significant to the biology of the native fishes in Grand Canyon after dam installation on the Colorado River and is an important spawning and nursery site for all 4 native fish species. It is also the most important (and perhaps exclusive) spawning site for the endangered humpback chub (Robinson et al., 1996; Valdez and Ryel, 1997; Stone, 1999). In addition, 6 nonnative fish species, i.e., 3 cyprinids (common carp *Cyprinus carpio* L., fathead minnow *Pimephales promelas* Rafinesque, and red shiner *Cyprinella lutrensis*, Baird and Girard), 2 ictalurid catfishes (channel catfish *Ictalurus punctatus* Rafinesque and yellow bullhead *Ameiurus natalis* Lesueur), and 1 cyprinodontid (plains killifish *Fundulus zebrinus* Jordan and Gilbert) have reproducing populations in the LCR. Stocked rainbow trout *Oncorhynchus mykiss* Walbaum, from Lees Ferry reach, a 26-km tailwater immediately below Glen Canyon Dam, are not uncommon in the LCR, whereas brown trout *Salmo trutta* L. are rarer.

Although previous studies have reported the distribution and host associations of *B. acheilognathi* and *L. cyprinacea*, the seasonal patterns of these parasites, as well as the parasite fauna of native and introduced fishes in Grand Canyon, in general, remain largely unknown. The importance of the LCR in sustaining the endangered humpback chub and at least 2 introduced parasites known to parasitize it, and the presence of nonnative fishes, made this river a natural site for a 2-yr seasonal study on the parasite fauna. The study addresses the characteristics of the parasite fauna, host–parasite associations, and seasonal patterns of parasitism in this unique ecosystem.

MATERIALS AND METHODS

Study area

The study area comprised the lower 18 km of the LCR to its confluence with the Colorado River at River Kilometer (RK) 98.6, within Grand Canyon, Arizona (Fig. 1). The LCR, with headwaters in the White Mountains of northeastern Arizona, has a length of 536.3 km and a drainage area of 69,790 km^2 (Oberlin et al., 1999). The major source of its perennial lower 22 km stretch is Blue Springs and a series of smaller springs, which together discharge approximately 6.3 m^3/sec of 20 C water that is supersaturated with calcium carbonate and charged with free CO_2 (Johnson and Sanderson, 1968; Cole, 1975). These carbonates give the LCR its characteristic aqua-blue color during base flow periods. Deposits of carbonates (mainly $CaCO_3$), known as travertine, form on the stream bottom, along stream banks, and on rocks, in turn encrusting vegetation and smothering the benthos. Travertine formations along the edges of riffles and rapids result in low travertine 'dams' and impede flow. During periods of flooding, usually in the monsoon season (July–September) and in the spring (February–April), the flow in the LCR can reach 3,400 m^3/sec (USGS: www.usgs.gov/nwis/). Vegetation along the stream bank is generally sparse and consists of stands of *Phragmites australis*, *Salix exigua*, and *Tamarix chinensis*.

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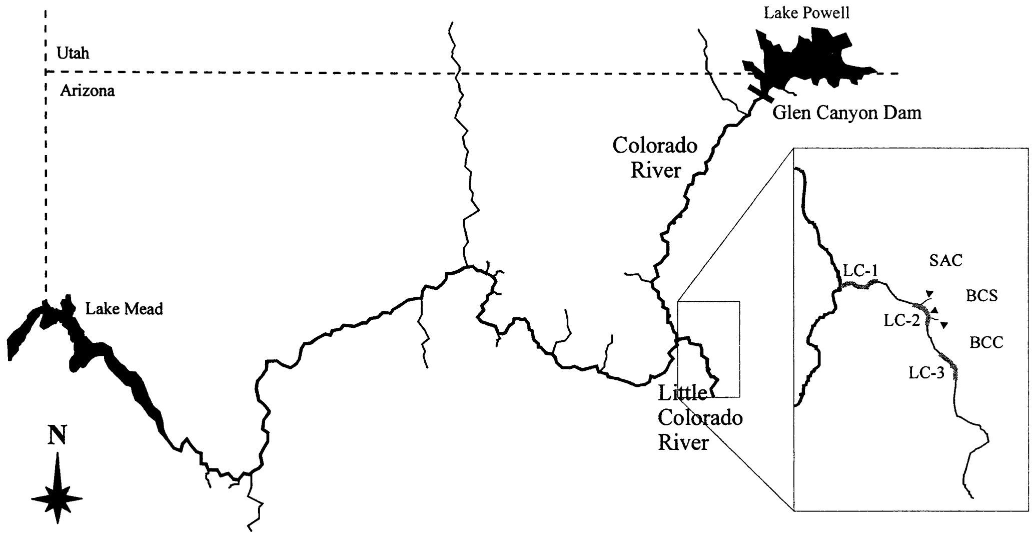

FIGURE 1. The Colorado River drainage and location of fish sampling sites in the LCR, Grand Canyon, Arizona. LC1 = RK 0–2.5; LC2 = RK 10.6–11.5; LC3 = RK 14.5–15.1; BCC, Big Canyon Creek; BCS, Big Canyon Springs; SAC, Salt Creek.

The 3 sampling reaches, on the lower 18 km of the LCR, were designated LC1, LC2, and LC3. The most upstream reach (LC3) was above the Atomizer/Chute Falls Complex, 13.6 RK upstream of the confluence with the Colorado River. This reach usually contains only speckled dace and nonnative common carp and fathead minnows (Robinson et al., 1996; D. Stone, pers. comm.) because of the waterfall barrier. This reach was only sampled once (September 1999) because river conditions did not permit helicopter landing on a regular basis. The middle reach (LC2, RK 10.6–11.5) is in the area of Salt Trail Canyon (RK 10.8) and contains all fish species that complete their life cycles in the LCR, as well as occasional rainbow trout (Robinson and Clarkson 1992; U.S. Fish and Wildlife Service, 1994). Two clear saline creeks, Big Canyon Creek (BCC) in Big Canyon and Salt Creek (SAC) in Salt Canyon, and a saline spring, Big Canyon Springs (BCS), drain into the LCR in this reach. These tributaries were also sampled. The most downstream reach (LC1) is in the vicinity of Boulder Camp (RK 2) and ranged from RK 2.5 to the mouth (RK 0). This reach contains all species present in the LCR, including those that move into the LCR from the Colorado River, such as rainbow trout and, more rarely, brown trout *S. trutta* (Robinson and Clarkson 1992; Arizona Game and Fish Department, 1996; Brouder and Hoffnagle, 1997). Nets and other sampling gear (see below) were set within a 1 km and 2.5 km stretch at LC2 and LC1, respectively.

TABLE I. Lengths, weights, and total number of fish examined in a study of the Lower Little Colorado River.

Fish species	Length* (mm)	Weight* (g)	N
Native			
Catostomus discobolus	84.48 ± 48.83 (35–288)	10.67 ± 23.32 (30–147)	148
Catostomus latipinnis	103.64 ± 86.46 (36–492)	50.89 ± 173.17 (0.5–962)	73
Gila cypha	93.55 ± 36.43 (34–232)	7.76 ± 10.27 (0.2–78.3)	116
Rhinichthys osculus	69.1 ± 12.12 (29–115)	2.97 ± 4.47 (0.2–85)	630
Nonnative			
Ictalurus punctatus	381.57 ± 212.71 (48–770)	1,147.68 ± 469.3 (0.8–8,030)	54
Cyprinus carpio	119.16 ± 133.83 (32–600)	139.64 ± 463.57 (0.5–2,617.5)	63
Pimephales promelas	61.97 ± 12.12 (31–99)	2.42 ± 1.61 (0.3–10.3)	193
Fundulus zebrinus	55.48 ± 9.4 (28–81)	1.67 ± 0.9 (0.4–5.5)	113
Oncorhynchus mykiss	326.14 ± 44.34 (252–441)	298.69 ± 133.14 (122–441)	22
Cyprinella lutrensis	60.18 ± 10.31 (50–88)	1.97 ± 0.89 (1–3.9)	11
Ameiurus natalis	165.42 ± 63.15 (80–252)	76.77 ± 63.84 (5.7–185)	12

* Mean ± SD (minimum–maximum). N = sample size.

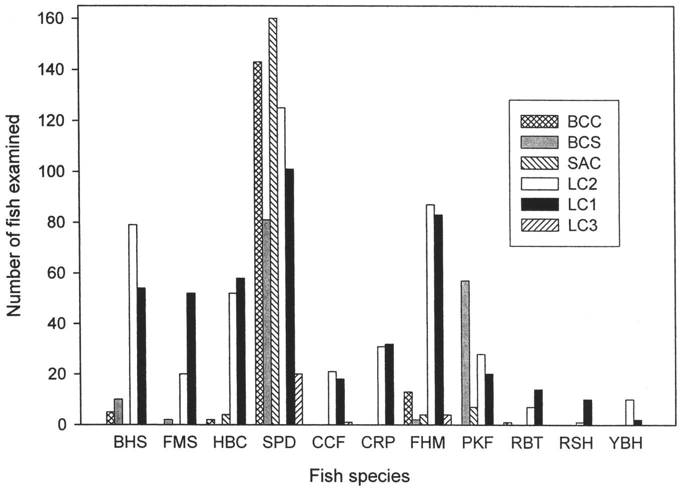

FIGURE 2. Number of individuals of different fish species examined from the different sampling sites. See Figure 1 and text for acronyms of sampling sites. BHS, Bluehead sucker; FMS, Flannelmouth sucker; HBC, Humpback chub; SPD, Speckled dace; CCF, Channel catfish; CRP, Carp; FHM, Fathead minnow; PKF, Plains killifish; RBT, Rainbow trout; RSH, Red shiner; YBH, Yellow bullhead.

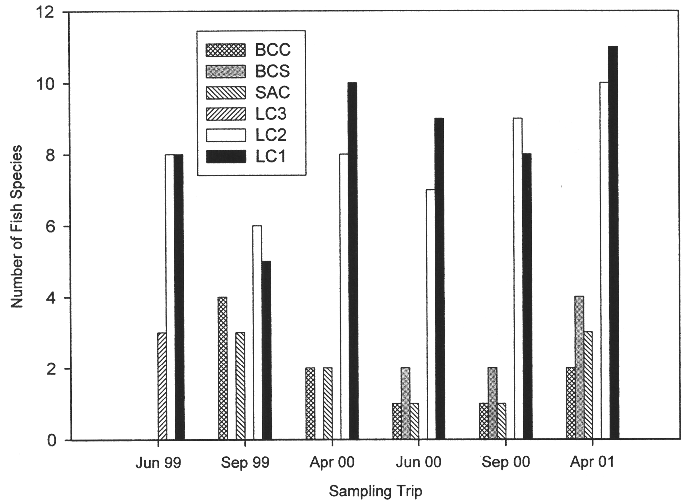

FIGURE 3. Number of species of fish recovered from the different sampling sites during the LCR study. See Figure 1 and text for acronyms of sampling sites.

Sampling

Fish: Most species were caught using medium (45 cm) and large (91 cm) hoop nets (each with 10 cm mouths and 6 mm mesh) and minnow traps (each with 25 mm mouth and 3 mm mesh). Six hoop nets of each size were deployed in each reach. Minnow traps were deployed in pods of 5 traps, comprising a total of 4 or 5 pods in each reach. One or 2 pods of minnow traps were set in the tributary creeks (BCC, BCS, and SAC), and only minnow traps were used at these sites. In addition, baited trot lines were used to catch channel catfish and rainbow trout. These 2 species were also taken by angling. Gill nets yielded few or no fish and were not used after September 1999. Seines were used less frequently to catch very small fish and mainly when the yield from other sampling gear was low. Hand-held sling spears and spear guns were used to capture carp and channel catfish along shallow shorelines. All gear were checked once a day and fish were brought back live to camp for necropsy. The relatively low numbers of the endangered humpback chub examined were due to restrictions on both sample size and fish size (U.S. Fish and Wildlife Service, Permit No. TE008513-0). During each trip (sampling period), a maximum of 10 individual chub could be taken for necropsy from each of the 2 reaches, LC1 and LC2. Fish had to be less than 150 mm, i.e., juveniles. Two larger chub (190 and 232 mm) that had died during the sampling were also examined and included in the analysis. This quota of 20 fish (10 per reach) per trip was met in most cases (Table II).

Fish were processed shortly after capture, or were held in 19-L buckets (with aerated water), or in live cars in SAC or in the LCR before processing. Fish were weighed and measured (total lengths) and necropsied using a binocular dissecting microscope.

Parasites: Parasites were fixed and preserved following methods in Van Cleave and Mueller (1932) and Pritchard and Kruse (1982). Briefly, parasites were killed and simultaneously fixed in heated or unheated fixatives (10% buffered or nonbuffered formalin, 70% ethanol). Platyhelminths, copepods, and leeches were stained in acetocarmine or Ehrlich's hematoxylin and processed for permanent slide mounts. Nematodes were cleared in a solution of 5% glycerin in 70% ethanol. Vouchers of the following species (accession numbers are in parentheses) have been deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland: *Henneguya exilis* Kudo, 1929 (USNPC 94573), *Ergasilus arthrosis* Roberts, 1969 (USNPC 94176), *L. cyprinacea* (USNPC 94158, 94177–94179, 94197), Oribatida gen. sp. (USNPC 94161–94163, 94175), *Myzobdella lugubris* Leidy, 1851 (USNPC 94196), *Gyrodactylus hoffmani* Wellborn and Rogers, 1971 (USNPC 94173), *Dactylogyrus extensus* Mueller and VanCleave, 1932 (USNPC 94172), *Ligictaluridus floridanus* (Mueller, 1936) (USNPC 94174), *Contracaecum* sp. (USNPC 94169, 94170), *Eustrongylides* sp. (USNPC 94159, 94160), *Rhabdochona* sp. (USNPC 94164–94166), *Truttaedacnitis truttae* (Fabricius, 1794) (USNPC 94167, 94168), *B. acheilognathi* (USNPC 94184–94187), *Corallobothrium fimbriatum* Essex, 1927 (USNPC 94188–94191), *Megathylacoides giganteum* (Essex, 1928) (USNPC 94192–94195), *Ornithodiplostomum* sp. (USNPC 94171, 94180, 94181), and *Posthodiplostomum* sp. (USNPC 94182, 94183).

Temperature recording: Water temperature was recorded with Hobo® Temp temperature data loggers (Onset Computer Corporation, Bourne, Massachusetts) in submersible waterproof, polycarbonate cases. Data loggers were deployed in SAC and BCC and programmed to record temperatures every 6 or every 12 hr continuously between 27 September 2000 and 6 June 2001. The BoxCar Pro 4.0 Program (for Windows) (Onset Computer Corporation) was used to program the Hobo Temp data loggers and retrieve data. Raw data were subsequently exported to a Microsoft Excel spreadsheet. Water temperature in the LCR between 1998 and 2001 was recorded by the USGS temperature gauge approximately 1 km upstream from the confluence with the Colorado River (William Vernieu, USGS Grand Canyon Monitoring Research Center, Flagstaff, Arizona, data not shown).

Analyses

The terms abundance, intensity, and prevalence follow definitions in Bush et al. (1997). Terms such as infracommunity, component community, and compound community follow definitions in Sousa (1994). The terms richness and diversity follow usage in Magurran (1988) and Peet (1974). Regression analyses and Pearson's correlation coefficient were used to examine relationships between fish length, parasite burden (total number of parasites in an individual fish), and infracommunity parasite species richness. Parasite community parameters examined included total component community richness, component community diversity (Shannon–Wiener's index), and mean (infracommunity) richness. Richness was compared using the Mann–Whitney *U*-test, and correlations were examined using Pearson's correlation and Spearman's rank correlation. Results of all tests (including regressions) were considered significant at $P < 0.05$. Zar (1996) was consulted for statistical methods.

RESULTS

Fish

In total, 1,435 fish belonging to 11 species (4 native, 7 nonnative) were examined (Table I). The term 'nonnative' refers to fish species that are not native to the Colorado River system, i.e., fishes that are native to other parts of the United States,

TABLE II. Parasites of native fishes in the Little Colorado River.*

	BHS (n = 148)	FMS (n = 73)	HBC (n = 116)	SPD (n = 630)
Parasite species				
Monogenea				
Gyrodactylus sp.	—	—	—	0.04 ± 0.44 (0–7) (0.01)
Cestoda				
Bothriocephalus acheilognathi	0.05 ± 0.58 (0–7) (0.01)	0.07 ± 0.48 (0–4) (0.03)	18.36 ± 34.55 (0–243) (0.84)	1.97 ± 6.06 (0–64) (0.43)
Corallobothriinae (pl.)†			0.009 ± 0.09 (0–1) (0.01)	—
Trematoda				
Ornithodiplostomum sp.† (v)	0.07 ± 0.59 (0–7) (0.03)	0.01 ± 0.12 (0–1) (0.01)	7.69 ± 20.67 (0–202) (0.67)	1.53 ± 3.36 (0–32) (0.4)
Ornithodiplostomum sp.† (b)			0.15 ± 0.46 (0–3) (0.11)	0.03 ± 0.19 (0–2) (0.03)
Ornithodiplostomum sp.† (e)			0.02 ± 0.13 (0–1) (0.01)	0.001 ± 0.04 (0–1) (0.001)
Posthodiplostomum sp.†	—	—	0.01 ± 0.09 (0–1) (0.01)	—
Unidentified metacercaria	0.006 ± 0.82 (0–1) (0.006)	—	0.009 ± 0.09 (0–1) (0.01)	0.003 ± 0.06 (0–1) (0.003)
Nematoda				
Rhabdochona sp.	—	—	0.11 ± 0.39 (0–2) (0.09)	0.37 ± 1.66 (0–23) (0.12)
Eustrongylides sp.†	—	—	—	0.001 ± 0.04 (0–1) (0.001)
Contracaecum sp.†	—	—	—	0.003 ± 0.06 (0–1) (0.003)
Acari				
Oribatida gen. sp.†	—	—	—	0.02 ± 0.18 (0–3) (0.02)
Crustacea				
Lernaea cyprinacea (adult female)	—	—	0.07 ± 0.25 (0–1) (0.01)	0.01 ± 0.11 (0–2) (0.01)
Lernaea cyprinacea† (copepodites)	—	—	0.03 ± 0.37 (0–2) (0.01)	0.008 ± 0.10 (0–2) (0.01)

* Mean abundance ± SD (minimum–maximum) (prevalence).
† Larval stages: pl, plerocercoid; v, viscera; b, brain; e, eye.

e.g., channel catfish, red shiners, etc., and to other continents, e.g., common carp. The 4 native fishes made up 67.4% of the total sample. Speckled dace comprised 43.9% of the total sample. All but 1 rainbow trout were caught from the LCR, and mostly in the downstream reach, LC1. Similarly, humpback chub were rarely caught from sites other than the LCR. BCC and SAC provided mainly speckled dace and occasionally a few other smaller species. BCS yielded mainly plains killifish and speckled dace (Fig. 2). In general, 2 reaches of the LCR (LC1 and LC2) consistently yielded a major proportion of the samples (Fig. 2), as well as the richest assemblage of fish species throughout the study (Fig. 3). High turbidity during the September 1999 sampling period made sampling difficult and a sudden flooding event forced an early termination of sampling at LC1. This is reflected in the poor returns from sampling in the LCR during that time.

Most species were sampled over a considerable size range (Table I). However, most (>90%) of the flannelmouth suckers examined were <100 mm long. Similarly, most of the bluehead suckers were also immature individuals. Species such as the red shiner, yellow bullhead, and common carp were caught more sporadically. Most carp samples were concentrated in 1 sampling period (June 2000), and these consisted largely of small immature individuals. Other fish species, including most of the channel catfish examined, were taken as older juveniles and adults (see lengths and weights in Table I).

Parasites

A total of 17 species of parasites was recovered (Tables II, III). The species of monogenean found in speckled dace closely resembles the species found in fathead minnow (except for minor differences in the dorsal bar) and may be conspecific with it, but has been treated separately because of condition of samples. Eleven of the 16 metazoan parasites were found as adults. Of these, *Rhabdochona* sp. was the only adult parasite native

TABLE III. Parasites of nonnative fishes of the Little Colorado River.*

	CCF (N = 54)	CRP (N = 63)	FHM (N = 193)	PKF (N = 113)	RBT (N = 22)	RSH (N = 11)	YBH (N = 12)
Parasites							
Myxozoa							
Henneguya exilis	P† (0.02)	—	—	—	—	—	—
Monogenea							
Ligictaluridus floridanus	1.13 ± 7.62 (0–56) (0.07)	—	—	—	—	—	—
Dactylogyrus extensus	—	0.27 ± 0.83 (0–4) (0.13)	—	—	—	—	—
Gyrodactylus hoffmani	—	—	0.24 ± 1.32 (0–15) (0.09)	—	—	—	—
Cestoda							
Bothriocephalus acheilognathi	0.04 ± 0.19 (0–1) (0.05)	3.5 ± 5.4 (0–28) (0.52)	0.84 ± 5.28 (0–72) (0.23)	1.26 ± 4.54 (0–26) (0.15)	0.04 ± 0.21 (0–3) (0.14)	1.2 ± 1.31 (0–3) (0.63)	0.08 ± 0.28 (0–1) (0.08)
Corallobothrium fimbriatum	1.97 ± 7.67 (0–56) (0.35)	—	—	—	—	—	—
Megathylacoides giganteum	1.59 ± 2.51 (0–10) (0.4)	—	—	—	—	—	—
Corallobothriinae‡	0.18 ± 1.12 (0–8) (0.02)	—	—	—	—	—	—
Trematoda							
Ornithodiplostomum sp.‡ (v)	0.02 ± 0.14 (0–1) (0.02)	—	0.24 ± 1.56 (0–17) (0.06)	—	—	—	—
Ornithodiplostomum sp.‡ (b)	—	—	0.01 ± 0.11 (0–1) (0.01)	—	—	—	—
Posthodiplostomum sp.‡	—	—	0.02 ± 0.36 (0–5) (0.005)	—	—	—	—
Nematoda							
Rhabdochona sp.	—	—	—	0.01 ± 0.09 (0–1) (0.01)	—	—	—
Truttaedacnitis truttae	—	—	—	—	24.8 ± 25.57 (0–108) (1)	—	—
Eustrongylides sp.‡ (l)	0.24 ± 0.58 (0–3) (0.18)	—	—	—	—	—	—
Contracaecum sp.‡ (l)	0.18 ± 0.55 (0–3) (0.13)	—	—	—	—	0.09 ± 0.30 (0–1) (0.09)	0.08 ± 0.29 (0–1) (0.08)
Acari							
Oribatida gen. sp.	—	—	—	0.18 ± 0.13 (0–1) (0.02)	—	—	—
Crustacea							
Ergasilus arthrosis	0.02 ± 0.14 (0–1) (0.02)	—	—	—	—	—	—
Lernaea cyprinacea (female)	—	—	—	0.01 ± 0.09 (0–1) (0.01)	—	—	—
Lernaea cyprinacea (copepodite)	—	—		0.005 ± 0.07 (0–1) (0.005)	0.12 ± 0.5 (0–3) (0.07)	0.04 ± 0.21 (0–1) (0.04)	

TABLE III. Continued

	CCF (N = 54)	CRP (N = 63)	FHM (N = 193)	PKF (N = 113)	RBT (N = 22)	RSH (N = 11)	YBH (N = 12)
Hirudinea							
Myzobdella lugubris	0.02 ± 0.14 (0–1) (0.02)	—	—	—	—	—	—

* Mean abundance ± SD (minimum–maximum) (prevalence).
† P, Present (prevalence).
‡ Larval stages: l, larva; pl, plerocercoid; v, visceral; b, brain.

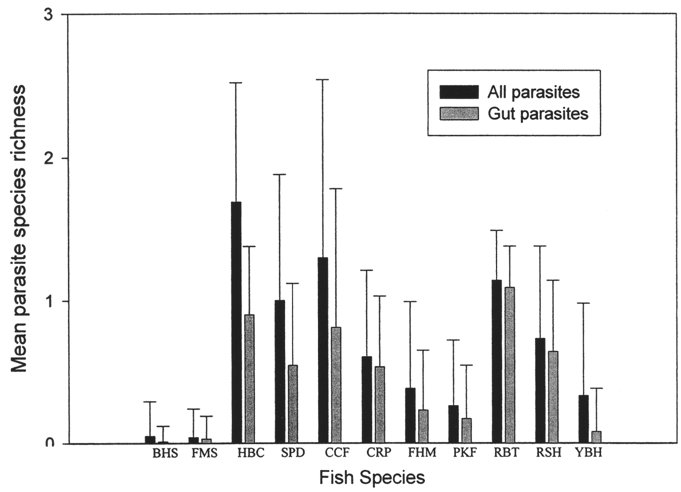

FIGURE 4. Mean parasite species richness of the different species of fishes examined in LCR study. See Figure 2 for acronyms of fish species.

to the LCR. All other adult parasite species were most likely introduced with their fish hosts. Parasites found as larval or juvenile stages mature in fish-eating birds (2 nematodes, *Contracaecum* sp., *Eustrongylides* sp. and 2 trematodes, *Ornithodiplostomum* sp., *Posthodiplostomum* sp.), in channel catfish (plerocercoids of Corallobothriinae), or in the aquatic environment (mites). Most of the adult parasites recovered were highly host specific (Tables II, III). *Bothriocephalus acheilognathi* was recovered in all fish species examined but was rare in the catostomids, rainbow trout, and ictalurids. The species of *Rhabdochona* from speckled dace appears to be previously unknown and is being described elsewhere. Gravid females of this nematode were not found in any other fish host in the LCR.

Component community richness was highest in channel catfish (7 species), but overall mean infracommunity richness was highest in humpback chub (1.86) followed by channel catfish (1.23). No common pattern of seasonal change in infracommunity richness was detected in the different fish species examined, except that both humpback chub and speckled dace showed lowest infracommunity richness values in the summer (June) sampling periods in both 1999 and 2000 (Table IV). The component and infracommunities of the 2 native sucker species were consistently species-poor (Fig. 4; Table II). Diversity of parasite component communities was remarkably uniform in humpback chub during the study period (Table IV) compared with assemblages in speckled dace and channel catfish. Furthermore, the overall diversity of chub parasite communities in LC1 and LC2 were nearly identical (Table V).

Bothriocephalus acheilognathi reached its highest abundance in humpback chub (Fig. 5; Table II). Abundance of *B. acheilognathi* showed a clear seasonality in humpback chub and was significantly lower in the summers than in any other time in this study (Fig. 6). Abundance values of the tapeworm were also consistently (and in most sampling periods significantly) higher at LC2 than at LC1 (Fig. 6). Except for abundance values of *B. acheilognathi* in chub from LC1 during April 2001, the 2 reaches of the river (LC2 and LC1) showed similar seasonal patterns (Fig. 6). This pattern was not mirrored by the infections of *B. acheilognathi* in speckled dace from any of the

TABLE IV. Parasite component community diversity* and infracommunity richness† in humpback chub, speckled dace, and channel catfish from the LCR.

	Gila cypha	*Rhinichthys osculus*	*Ictalurus punctatus*
Sampling period			
June 1999	0.22 (0.47) (N = 19)	0.27 (0.57) (N = 86)	0.36 (0.59) (N = 10)
	1.0 ± 0.74	0.53 ± 0.68	2.0 ± 1.15
September 1999	0.28 (0.47) (N = 18)	0.42 (0.89) (N = 99)	0.50 (0.65) (N = 11)
	1.73 ± 0.93	1.06 ± 0.83	1.54 ± 1.29
April 2000	0.25 (0.53) (N = 20)	0.37 (0.48) (N = 97)	0.58 (0.69) (N = 12)
	1.6 ± 0.59	1.37 ± 0.87	1.42 ± 1.38
June 2000	0.26 (0.55) (N = 20)	0.51 (0.72) (N = 113)	0.50 (0.6) (N = 7)
	1.35 ± 0.81	1.02 ± 0.77	1.85 ± 1.46
September 2000	0.31 (0.44) (N = 20)	0.49 (0.63) (N = 111)	0.35 (0.48) (N = 13)
	2.25 ± 0.63	1.22 ± 1.01	0.61 ± 0.96
April 2001	0.29 (0.47) (N = 20)	0.38 (0.55) (N = 124)	
	2.22 ± 0.42	0.81 ± 0.83	

* Shannon–Wiener index (Shannon's H') followed by evenness (in parentheses) and the sample size (N) of hosts in parentheses.
† Mean infracommunity richness ± SD.

sampling sites (Fig. 7). Abundance of *B. acheilognathi* infections in speckled dace was significantly higher in BCC throughout the study than in any other location (Fig. 8). Of the 2 creeks, a seasonal pattern of tapeworm abundance was only observed in BCC, where abundance values of the tapeworm were significantly higher in the spring and lower in the fall and summer (Fig. 8). In total, 3,930 individuals of *B. acheilognathi* were recovered in this study. Of these, 2,130 (or 54.1%) were found in humpback chub. Regression analyses showed that, overall, there was a positive correlation between length of humpback chub and tapeworm burden (overall $R^2 = 0.12$), but R^2 values varied from as low as 0 (September 1999) to 0.19 (April 2000).

Abundance of *Ornithodiplostomum* sp. also followed trends in humpback chub that were similar to those seen with *B. acheilognathi* (higher abundance values in the fall) (Fig. 9). *Ornithodiplostomum* sp. also shows significantly higher abundance values in BCC than elsewhere (Fig. 10). Regression analyses indicated that, overall, infections of *Ornithodiplostomum* sp. (worm burden) were positively and significantly correlated with body size of humpback chub ($R^2 = 0.28$), but R^2 values varied between a low of 0.03 (not significant) (September 1999) and a maximum of 0.75 (September 2000) (significant).

Temperature

Temperature profiles were generated from the temperature data recorded by the Hobo® Temp data loggers for BCC and SAC (Fig. 11) and for the LCR from the data recorded by the USGS temperature data logger (Fig. 12). The sharp decrease in temperatures in both SAC and BCC near the end of October (Fig. 11) was possibly due to a flooding event in Salt Canyon and Big Canyon.

TABLE V. Parasite component community diversity* in humpback chub and speckled dace at different sampling sites in the LCR.

	Gila cypha	*Rhinichthys osculus*
Sampling site†		
LC1	0.27 (0.44) (N = 58)	0.46 (0.59) (N = 101)
LC2	0.29 (0.38) (N = 52)	0.55 (0.81) (N = 125)
BCC	—	0.35 (0.51) (N = 143)
BCS	—	0.50 (0.65) (N = 81)
SAC	—	0.43 (0.56) (N = 160)

* Shannon–Wiener index (Shannon's H') followed by evenness (in parentheses) and the sample size (N) of hosts in parentheses.
† See Figure 1 for sampling sites.

DISCUSSION

Fifteen of the 17 species of parasites identified in this study (Tables II, III) are first published records for the LCR and for the Colorado River drainage in Grand Canyon. *Bothriocephalus acheilognathi* and *L. cyprinacea* have been reported from the LCR and other sites in the Grand Canyon (Carothers et al., 1981; Brouder and Hoffnagle, 1997; Clarkson et al., 1997; Hoffnagle and Cole, 1999). The parasite assemblage is unique in having only 1 species of native adult helminth, i.e., the 'new' species of *Rhabdochona* in speckled dace, and the native parasite fauna is species-poor and occur with low abundances. The parasite assemblage was numerically dominated by parasites introduced by nonnative fish (as in *B. acheilognathi*) or by piscivorous birds (as in *Ornithodiplostomum* sp.). This follows the spillover patterns seen in other systems involving introduced parasites (Leong and Holmes, 1981). Exchange of adult parasites among hosts appears to be rare, and host specificity or host preferences observed in this study follow patterns of associations elsewhere (Hoffman, 1999). Although *B. acheilognathi* was found in all fish species examined, it clearly has a predilection for cyprinids. This is in keeping with its known host preferences (Bauer, 1991; Kennedy, 1991; Scholz, 1997, 1999; Hoffman, 1999).

The parasite fauna in the LCR is also unusual in lacking adult trematodes. Instead, there are only larval strigeids (*Ornithodiplostomum* sp. and *Posthodiplostomum* sp.) that are likely transmitted by the only species of mollusk, *Physa pilsbryi*, in the LCR and its tributaries (data not shown). This explains why trematodes such as lissorchiids and macroderoidids, generally characteristic of catostomids and ictalurids, respectively (Hoffmann, 1999), are not found in these fishes in the LCR. Periodic flooding causes at least periodic reduction of the invertebrate fauna (potential intermediate hosts) from the river. Recoloni-

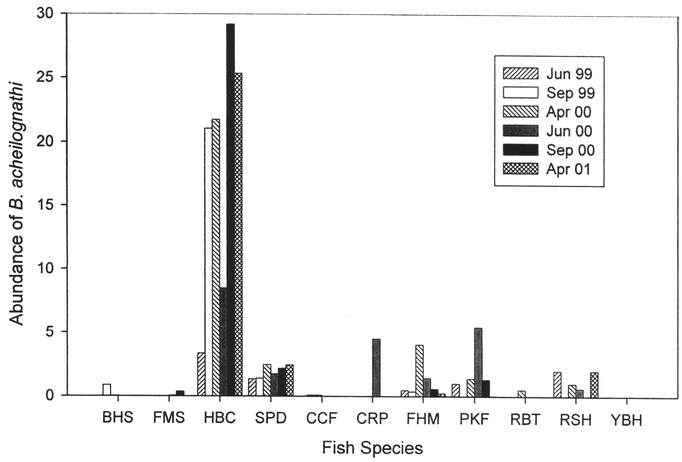

FIGURE 5. Abundance of *Bothriocephalus acheilognathi* in 11 species of fishes in the LCR at different sampling periods. Acronyms of fish species as in Figure 2.

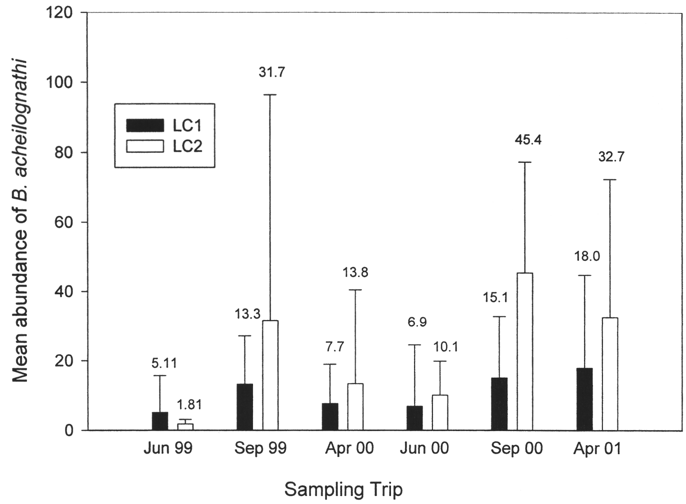

FIGURE 6. Abundance of *Bothriocephalus acheilognathi* in humpback chub in LC1 and LC2 at different sampling periods. Acronyms of sampling sites as in Figure 1.

zation by benthic macroinvertebrates is made difficult because of extensive travertine deposition that smothers the benthos and encrusts vegetation and rocks. Such inherent instability is also likely to promote relatively short links in the trophic web that, in turn, impact parasite circulation. Four species (*Contracaecum* sp., *B. acheilognathi*, *C. fimbriatum*, and *M. giganteum*) are transmitted to their fish hosts (at least to the first fish host) by copepods. Ten species (*H. exilis*, *L. cyprinacea*, *E. arthrosis*, *M. lugubris*, *Ornithodiplostomum* sp., *Posthodiplostomum* sp., the oribatid mite, and the 3 [or 4] species of monogeneans) infect or infest their fish hosts by direct attachment of larvae or by penetration. Seven of these do not use any prior intermediate host. Only 2 species, *Rhabdochona* sp. and *Eustrongylides* sp., are transmitted by benthic macroinvertebrates in the diet. *Eustrongylides* spp. use tubificid oligochaetes as intermediate hosts as do myxozoans, whereas *Rhabdochona* spp. commonly have some insect larvae (e.g., ephemetropterans) as intermediate hosts (Anderson, 2000). The physical nature of the river may also explain why the ectoparasites were so sporadic in occurrence and relatively rare in the system.

The parasite fauna of the LCR is also unusual in being species-poor in native fishes. The 2 native catostomids (bluehead sucker and flannelmouth sucker) had parasite faunas that were exceptionally depauperate for catostomids (Margolis and Arthur, 1979; McDonald and Margolis, 1995; Hoffman, 1999). Higher infracommunity richness in humpback chub and speckled dace was a result of the high prevalences of *B. acheilognathi* and *Ornithodiplostomum* sp. (resulting in higher evenness values) rather than high component richness. The parasite fauna of some of the nonnative fishes, e.g., channel catfish, was also species-poor and reduced in taxonomic diversity compared with the fauna in their native range (Hoffmann, 1999). Rainbow trout, which were stocked from hatcheries instead, have only 1 parasite specific to them (and other salmonids), viz. *T. truttae*, in the LCR. The finding of *T. truttae* of various sizes in rainbow trout in the Grand Canyon indicates that the life cycle is well established there. Brook lampreys are considered to be obligate intermediate hosts of this parasite in Europe, and brown trout in Europe become infected by ingesting lampreys (Moravec, 1994). Because there are no lampreys in the Colorado River in Grand Canyon, some other intermediate host is involved. Choudhury and Dick (1996) showed that there was a morphological difference between North American and continental European *T. truttae*. This study highlights the fact that there are biological differences as well.

The abundance of the numerically dominant parasite, *B. acheilognathi*, in nonnative cyprinids such as fathead minnows, red shiners, and small carp, as well as in the plains killifish, implicates any of these fishes as hosts that introduced the tapeworm into the LCR. It is possible that bait bucket transfers into the upper reaches of the LCR or into the Colorado River may have been responsible for the introductions. The data on *B. acheilognathi* infections in this study (Figs. 6–8; Tables II, III) demonstrate the high colonizing potential of this parasite. This is in keeping with its establishment in nonnative areas worldwide (Boomker et al., 1980; Bauer, 1991; Kennedy, 1991; Esch and Fernandez, 1993; Heckmann et al., 1993; Font and Tate, 1994; Pérez-Ponce de León et al., 1996; Dove et al., 1997; Hoffman,

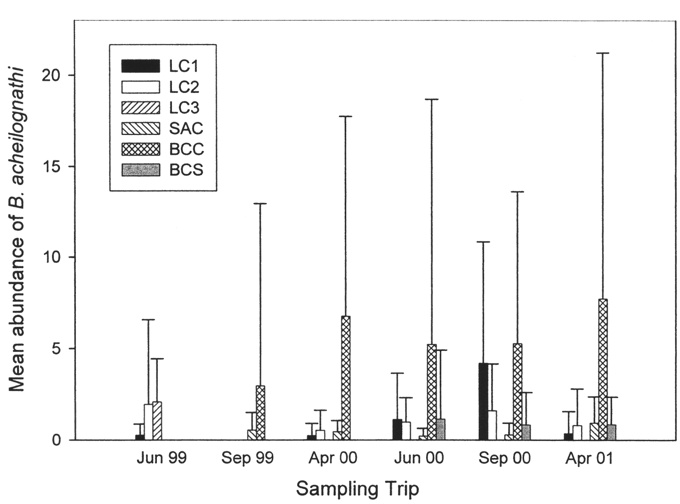

FIGURE 7. Abundance of *Bothriocephalus acheilognathi* in speckled dace at different sampling sites at different periods.

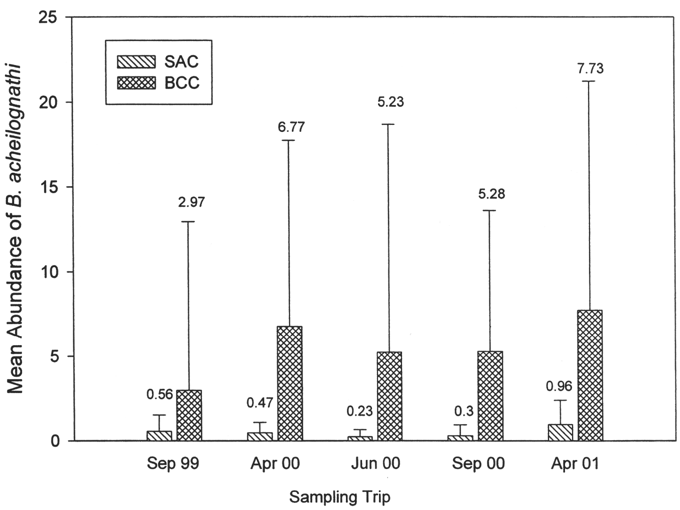

FIGURE 8. Abundance of *Bothriocephalus acheilognathi* in speckled dace in Big Canyon Creek (BCC) and Salt Creek (SAC) at different sampling times.

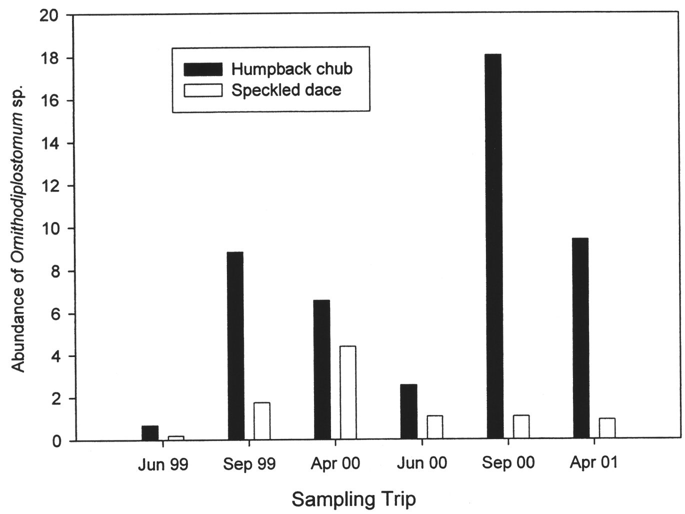

FIGURE 9. Abundance of *Ornithodiplostomum* sp. in humpback chub and speckled dace from different sampling periods.

1999). Comparisons of *B. acheilognathi* infections with past studies (Brouder and Hoffnagle, 1997; Clarkson et al., 1997) show that the parasite is well established in native cyprinids, i.e., humpback chub and speckled dace. Although chub comprised only 8% of the total number of fish examined in this study, it harbored 54.1% of the tapeworms recovered, making it the most important host in the LCR (Fig. 5). These findings are in contrast to those of Dove (1998), who found that exotic fishes (carp) were the main hosts of *B. acheilognathi* in Australia, both in terms of numbers and biomass of the tapeworm. Dove also predicted that *B. acheilognathi* required carp as a reservoir host for the infections to be maintained in native fishes in Australia. This is possibly due to the fact that Australia has a unique and isolated freshwater fish fauna, devoid of native cyprinids (Nelson, 1994). Our study suggests that *B. acheilognathi* would persist and maintain its presence in the LCR even in the absence of carp or other nonnative hosts.

A combination of behavioral and physiological traits may make humpback chub suitable hosts of *B. acheilognathi*. First, chub are omnivores (Valdez and Hoffnagle, 1999), and zooplankton comprises a large percentage of their diet (AZGF, 1996). They commonly feed on copepods even as larger juveniles. Adult humpback chubs prey on small cyprinids including their own species (Stone, 1999), which may facilitate infection in larger fish via infected copepods in the stomachs of prey fish. Second, as a native species, the humpback chub is well adapted to exploit habitat and food in the LCR. Speckled dace are also native, but they are primarily benthivores (AZGF, 1996), as reflected by the presence of *Rhabdochona* sp. Although dace are suitable hosts of *B. acheilognathi*, their foraging behavior may prevent heavier infections. Finally, the humpback chub is a much larger species than the speckled dace. Whereas this in itself should not necessarily mean higher infections in humpback chub, ingestion of large concentrated amounts of zooplankton indirectly through predation on small planktivorous fish, and its omnivorous feeding in the water column, may expose it to infected zooplankton at all stages in its life history. However, the restriction of our sampling to chub less than 150 mm prevents firm conclusions about the transmission dynamics of *B. acheilognathi* in larger fish.

Seasonal patterns of infection with *B. acheilognathi* were observed in humpback chub in both reaches (LC1 and LC2) of the river (Fig. 6). The general trend was lowest abundance in the summer months with significantly higher abundance values in the following fall (September). Temperature-related dynamics of *B. acheilognathi* have been demonstrated in the past (Granath and Esch, 1983a, 1983b; Marcogliese and Esch, 1989a, 1989b). The LCR provides the tapeworm with the temperatures necessary for its development and maturation, mainly during the summer months (Fig. 12), but the low abundance of worms in the summer (Fig. 6) may be related to seasonal changes in copepod abundance (see Marcogliese and Esch, 1989a). In addition to seasonal patterns, the data also revealed spatial differences in abundance of *B. acheilognathi* infections in

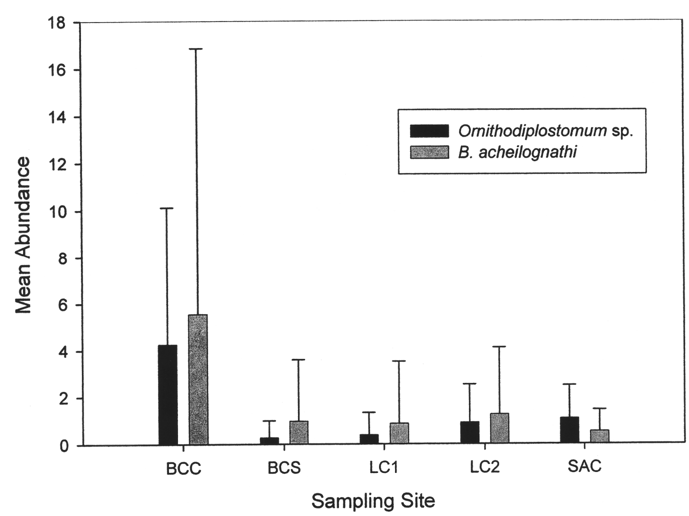

FIGURE 10. Abundance values of visceral *Ornithodiplostomum* sp., in speckled dace from different sampling sites. Corresponding abundance values of *Bothriocephalus acheilognathi* are provided for comparison. See Figure 1 for site acronyms.

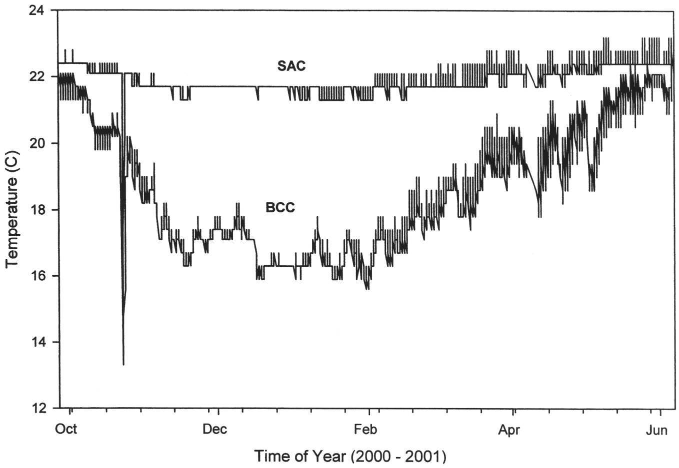

FIGURE 11. Temperature profiles of Big Canyon Creek (BCC) and Salt Creek (SAC), 27 September 2000 to 6 June 2001.

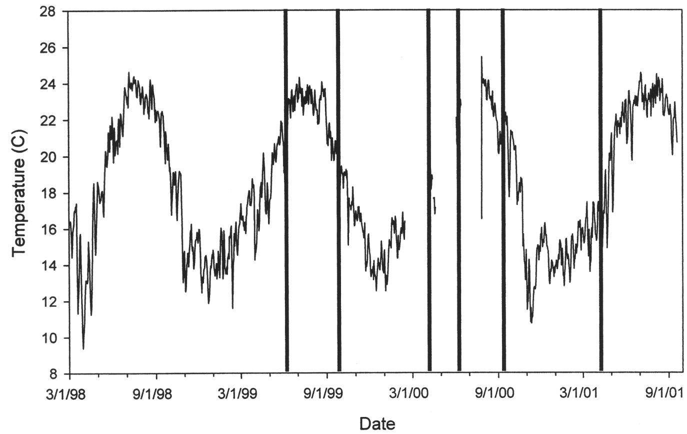

FIGURE 12. Mean daily temperature of the LCR at RK 1.2. Blank section is due to instrument failure after a flood. Shaded bars are sampling trips.

humpback chub (Fig. 6). The higher abundance values of tapeworm infections in the upper reach (LC2) as compared with the LC1 may be because of the presence of both creeks (BCC and SAC) and BCS in the LC2 reach, which provide landscape diversity and ideal habitat for copepods. Of these habitats, BCC may be particularly important. Although humpback chub were rarely caught in BCC (2 of 116 fish, with 243 and 45 tapeworms), access to such creeks may expose fish to functional reservoirs of infection, maintained by the dace in the creeks. Furthermore, the creeks may serve as refugia for copepods, intermediate hosts of *B. acheilognathi*, during flooding episodes in the LCR and as such serve as sources for the rapid colonization by copepods of the nearshore backwater environments in the LCR after base flows return to normal levels. The absence of such creeks in the lower reaches of the LCR precludes such opportunities.

Significantly higher abundance of *B. acheilognathi* in speckled dace in the larger of the 2 creeks, BCC (Fig. 8), is possibly related to larger populations and higher densities of dace ($\bar{x}$ CPUE [catch per unit effort]: 180.1 dace/24 hr in BCC vs. 52.2 dace/24 hr in SAC) and copepods because SAC apparently provides year-round temperatures suitable for transmission (Fig. 11). In BCC, the pattern clearly indicates low points in the summer and fall, which contrasts with the pattern shown by the parasite in dace in the LCR (Fig. 7), where high fall (September 2000) values are flanked by low summer and spring values. Temperature-dependent increases in spring infection values (abundance) from those of the previous respective fall lows (Fig. 7) is supported by the temperature profile of BCC (Fig. 11).

Seasonal changes in abundance were also evident in *Ornithodiplostomum* sp., the other abundant parasite in this system. An increase in abundance in the fall from preceding summer levels and a decrease in the subsequent spring is evident in both seasonal cycles of this study (Fig. 9). Significantly higher abundance of *Ornithodiplostomum* sp. in dace was also found in the larger of the 2 tributary creeks (BCC) (Fig. 10). Whether these seasonal and habitat patterns correlate with habitat use by nesting or feeding piscivorous birds and (or) the abundance of the mollusk intermediate host (*Physa* sp.) is open to further investigation. The metacercariae have been shown to alter visually mediated behavior in fish, increasing risk to predation and affecting foraging success (Sho and Goater, 2001). Its presence in chub and dace indicates that this parasite needs to be monitored as well.

This study demonstrates the intricate interplay between hosts, parasites, and habitat in a species-poor yet clearly complex system. The high colonizing potential of *B. acheilognathi* is reflected in its ability to infect a variety of fishes and habitats in the LCR and in its abundance in 2 native cyprinids. The study also demonstrates the importance of perennial tributary creeks as reservoir areas for copepods and fish and, consequently, for *B. acheilognathi*. Sustained and continued studies thus become critical in assessing future impacts of this and other parasites and an important issue in maintaining the biotic integrity of the Grand Canyon ecosystem. The scope of such studies must be broadened to include the Colorado River main stem, its tributaries, and warmer feeder creeks that may be critical to the success of these parasites. Monitoring fishes in both systems would provide information on the entire distribution of these parasites within the Grand Canyon and document whether the parasites spread as alternate flow regimes from Glen Canyon Dam and other management or remedial strategies are executed.

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